An ethological analysis of the reproductive behaviour of the bitterling (Rhodeus amarus Bloch.)

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the fact that these movements are performed with respect to the mussel and not with respect to other bitterlings.

b. The agonistic movements as "typical compromises".
It is reasonable to assume that originally the agonistic behaviour of the animals consisted of only two movements: chasing and fleeing. If so, the original state of the animals must have been characterized by a low level of integration of the aggressive and flight mechanisms. The development of the integration of these two mechanisms in the course of evolution may have made possible the performance of a number of agonistic movements corresponding with an equal number of A/F ratios. Because a restricted number of different agonistic movements is observed while numerous different A/F ratios are conceivable, it may be that the development of the integration of the A and F mechanisms has involved the development of "typical compromises" as described by MORRIS (1957). The definite agonistic movements seem to correspond indeed with definite ranges of the A/F ratios.

A useful discussion of the role of "typical intensities" and of "typical compromises" as factors in the evolution of the different reproductive movements of the bitterling would require more adequate data on the occurrence and the causation of these movements in a number of related species of bitterlings.

VIII. SUMMARY

This paper gives an analysis of the causation of the reproductive behaviour of the bitterling (*Rhodeus amarus* Bloch).

The non-reproductive and the reproductive behaviour of males and females have been described (chapter II and III) and a number of movements and postures typical of the bitterling have been selected for quantitative analysis. The temporal association during the reproductive period of 12 of these behaviour patterns was examined statistically and the correlations obtained were subjected to factor analysis (chapter IV, 2 and 3). Factor analysis demonstrated the existence of 3 independent common factors accounting for 80–90 % of the common variance among these behaviour patterns. Three groups of movements have been distinguished that are characterized by common factors and that are typical of the male.

(1) The agonistic group, characterized by the presence of two independent tendencies, the aggressive and flight tendencies, and including: fleeing, jerking, turning beats, head butting and chasing.

(2) The sexual group characterized by the sexual tendency and including: quivering, leading, head-down postures and skimming.

(3) The non-reproductive group characterized by feeding-, comfort- and flight tendencies and including snapping, chafing, finflickering and fleeing.

Factor analysis and non-factorial evidence show that the agonistic movements can be ranked according to an increasing A/F ratio (chapter IV, 4, a). Non-factorial evidence suggests the existence of two different internal mechanisms in the males; one for aggression and one for flight, both being stimulated by the presence of other males and, probably, by the presence of the mussel (chapter IV, 4, a).

Non-factorial evidence suggests the existence of an internal mechanism underlying the occurrence of the sexual movements. This mechanism is stimulated by the presence of a ripe female and of a mussel (chapter IV, 4, b).

Concerning the non-reproductive movements the result of factor analysis is consistent with the correlations found between these movements during the non-reproductive period. It is concluded that snapping on the one hand and chafing and finflickering on the other represent two different tendencies (chapter II and IV, 4, c).

The interaction between the internal mechanisms underlying the aggressive, flight and sexual tendencies has been examined by analysing the behaviour changes of a territorial male during spawning. Experiments show that the perception of the smell of the freshly laid eggs stimulates the aggressive and the sexual mechanisms of the male.

The decrease of the tendency to eject sperm after egg laying can be explained by the strong increase of the frequency of skimming in this period, while the decrease of quivering after egg laying has to be attributed to the high activation of the aggressive mechanism that inhibits quivering during this period. The increase of the frequency of skimming and, probably, of head-down postures after egg laying is independent of the high activation of the aggressive mechanism after egg laying. This is supported by experiments in which the A/F ratio of males was changed experimentally while the sexual behaviour was recorded. Tail bending – another sexual movement – proved to be less inhibited by an increase of the A/F ratio than quivering (chapter V).

Therefore it is concluded that (i) the degree at which the sexual movements of the male are expressed is dependent on the A/F ratio and (ii) this ratio has a differential influence on the performance of the sexual movements.

The tendencies of snapping, chafing and finflickering are negatively correlated with the aggressive and sexual tendencies which probably refers to inhibitive relations existing between the corresponding underlying mechanisms. The performance of snapping and of chafing at the mussel is probably facilitated by the performance of the sexually mo-

tivated head-down postures at the mussel. Finflickering is facilitated by situations that stimulate finspreading and finfolding simultaneously. The frequency of chafing increases when the aggressive and sexual tendencies are about equally high (chapter VI).

After a short discussion of the usefulness of factor analysis in motivation studies it is concluded that this method has many advantages over the usual methods (chapter VII, 1).

The differential effect of increases of the A/F ratio on the tendencies of the sexual movements is discussed and it is concluded that: (1). The inhibitive effect of A on S is not a unitary one, *i.e.* it acts on factors specific for and underlying the occurrence of the separate sexual movements and not on the common factor of these movements. In this context the disadvantages are discussed of working with common factors that have been determined by measuring one variable only. (2) The differential effect of A on S explains the difference of the sexual behaviour of both sexes, because the mean A/F ratio is different for males and females (chapter VII, 1).

The term consummatory act has been discussed critically and three basic models are suggested serving the analysis of behaviour changes (chapter VII, 2).

A superficial comparison of the behaviour of *Rhodeus amarus* and of *Rh. ocellatus* has been made and the derivation of some reproductive behaviour patterns of the bitterling is shortly discussed.

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